A FLORISTIC COMPARISON OF LOWER CAPE COD, MASSACHUSETTS AND THE NORTH CAROLINA OUTER BANKS

C. JOHN BURK[1]

Cape Cod, Massachusetts, and the Outer Banks of North Carolina are sandy, seaward extensions of the eastern North American landmass which have long been recognized as major points of demarkation in the distribution of marine floras and faunas. The phytogeographic relationships of the vascular floras of these two areas have not, however, been investigated. The purpose of this paper is to compare their modern floras, relating the comparison, so far as possible, to geologic and historical events through the last glaciation to the present, and to evaluate the significance of Cape Cod and the Outer Banks as distributional boundaries for vascular plants. The study is based largely on my own work on the Outer Banks (Burk, 1961) and the recent study of H. R. Hinds (1966) of lower (or "outer") Cape Cod.

Both Cape Cod and the Outer Banks originated, in their present form, as a consequence of the last glaciation, prior to which sea level stood about 25 feet higher than at present, submerging the landmass at both sites completely (Chamberlain, 1964; Richards, 1950). As the glacier formed and moved southward, sea-level dropped from 250 to 360 feet below its present level and Cape Cod was deposited as a series of moraines. Whitehead (1966), evaluating the recent arguments for and against marked displacement of plant community types by the glacier, concludes that a major southward displacement of many boreal species and profound climatic changes can no longer be disputed but that the concept of a zonal displacement of boreal and deciduous forest formations is still open to question.

---

[1]The author is indebted to Dr. Elizabeth B. Horner, Dr. Albert Radford, Dr. Marshall Schalk, and Dr. Kenneth Wright for their suggestions and critical readings of this manuscript.

At full-glacial time, a continuous coastal plain from Florida to Cape Cod was exposed. At the latitude of the Outer Banks, this plain was an estimated 90 miles in width; its vegetation can be partially reconstructed from palynological studies of the Dismal Swamp, Virginia, and southeastern North Carolina. There are appreciable differences between these two areas (Whitehead, 1966). The forests of Virginia were apparently more boreal in aspect — spruce was possibly the dominant tree and fir was probably not uncommon. In southern North Carolina at this time, red or jack pine (perhaps both) were apparently the dominant species; spruce was much less abundant and fir was very uncommon. A number of northern species including *Lycopodium lucidulum*, *L. annotinum*, *Schizaea pusilla*, and *Sanguisorba canadensis* occurred. It is possible pines were more abundant in this region simply as a result of the prevalence of coarse sands.

As the glacial ice melted, the sea-level rose. The seaward landmass was flooded and the "Provincelands hook" and various sandpits were added to Cape Cod from eroded materials which had previously lain beneath the sea. North of Boston, the level of the initial submergence lies above the present sea level; south of Boston, it is well below (Schafer and Hartshorn, 1966). Hence Cape Cod has not been flooded since the retreat of the glacier; the width of the Cape has, however, diminished markedly. At present, the Great Beach facing the Atlantic is being undermined at a rate of 3 1/2 feet per year (Chamberlain, 1964).

Davis (1965), evaluating various studies of the Pleistocene in northeastern United States, concludes that, following the retreat of the Wisconsin ice, a vegetation floristically similar to sub-arctic vegetation developed in New England. Trees were absent or infrequent for over 2000 years. About 11,500 years ago the climate apparently changed and forest vegetation began to develop in southern New England. Boreal species were abundant at first, with spruce contributing a high proportion of the pollen rain for 2,000 years. By about 8,000 years ago, temperate deciduous trees had become more abundant. There is evidence for a recent interval warmer than the present (Deevey and Flint, 1957; Raup, 1937). Raup suggests that *Chamaecyparis thyoides* may have passed an optimum on the coast and argues that the New England sprout hardwoods are persisting under fundamentally adverse conditions and may, in the normal course of succession, be greatly restricted or replaced by more northerly occurring species.

The greater part of the Outer Banks was created during the period of rising sea-level as a result of local erosion of the sediments of the recently inundated coastal plain by onshore waves. It is not impossible that a few sites on the Outer Banks (most probably, in this writer's opinion, the areas near Nagshead and Cape Hatteras) were exposed throughout this last rise. These sites might then have served as focal points for the subsequent formation of barrier bars and islands and provided refugia for terrestrial plants. The full glacial forests in North Carolina were replaced by forests with abundant oak, hickory, birch, hemlock, beech, elm, and other thermophilous species (Whitehead, 1966); by the close of late-glacial time, the forests were dominated by oak, hickory, and other deciduous species while percentages of hemlock and beech declined. In southeastern North Carolina, an oak-hickory forest type had attained maximum development by early postglacial time, considerably earlier than in southeastern Virginia. Subsequently *Nyssa* and *Taxodium* became more abundant.

There is little evidence to suggest what may have grown on the Outer Banks during the height of the thermal maximum, if such a period existed. Many of the dominant forest species on the Outer Banks persist markedly southward and it is possible that the species composition of the Outer Banks forests was not greatly altered during this time.

Table 1 summarizes climatic data from Cape Cod, the Outer Banks, and inland areas immediately adjacent to each. Cape Cod is colder and to some extent drier than the

Outer Banks; Provincetown has a growing season 89 days shorter than Cape Hatteras, a January average 15 degrees lower, a July average 11 degrees lower, and greater thermal maxima and minima. Both areas have milder climates than areas immediately inland or directly north or south from them.

The sandy soils of Cape Cod are, except for the Provincelands hook and various sandpits, glacial in origin; the sands of the Outer Banks are almost entirely marine. As Boyce (1954) noted, the vegetational structure of the two areas is remarkably similar, a sequence, inward from the open beach, of zonal plant communities from salt-spray tolerant dune grasses and herbs to a tangle of shrubs, vines, and small trees, to a forest which is relatively unaffected by the windborne salt spray. Tidal marshes are common to both areas and, on the Outer Banks, where the bars and islands are separated from the mainland by shallow, more or less enclosed sounds, they are a regular feature of almost any transect drawn from the ocean beach across the bank. On Cape Cod, open salt water brackets the landmass and saltmarshes occur in areas protected by sandspits and in estuaries. Freshwater ponds and pools are more common on Cape Cod as a result of the numerous "kettleholes" formed by the melting glacier.

On the Outer Banks, hurricanes are a major environmental force (Engels, 1952; Burk, 1961). Few hurricanes reach Cape Cod although other storms, primarily winter northeasters (Chamberlain, 1964) may be quite destructive there. Fire is a more important environment factor on Cape Cod than on the Outer Banks.

Much of Cape Cod, unlike the Outer Banks, has been intensively cultivated, and stages of old field succession are relatively common.

FLORISTIC COMPARISON

Neither Cape Cod nor the Outer Banks possess endemic species of vascular plants. The species which comprise their floras range, for the most part, both northward and southward as well as inland, often in different ecological

Table 1. Summary of climatic differences between Cape Cod, the Outer Banks, and inland stations adjacent to each.*

		TEMPERATURE		Degrees F				
Station	Annual precipitation (in.)	January av.	July av.	Max.	Min.	Last spring frost	Earliest fall frost	Growing season (days)
Provincetown (Cape Cod)	39.23	31.6	67.0	104	-8	Apr. 17	Nov. 3	200
Springfield (inland, Mass.)	41.27	27.3	73.2	104	-18	Apr. 27	Oct. 15	171
Hatteras (Outer Banks)	48.59	47.1	78.2	93	8	Feb. 27	Dec. 13	289
Belhaven (inland, N.C.)	50.63	46.0	79.9	106	0	Mar. 29	Nov. 7	223

*Data from U.S.D.A. 1941 Yearbook, *Climate and Man*

Table 2. Native species, genera, families, and orders occurring on lower Cape Cod, the Outer Banks, taxa shared by both areas, and an index of resemblance*.

	Species	Genera	Families	Orders
Lower Cape Cod	586	280	97	42
Outer Banks	462	277	106	43
Shared (both native)	183	170	84	39
Index	39.6	61.4	86.6	92.9

*see text

situations. *Pinus rigida,* for example, a dominant tree in fire-influenced forests on Cape Cod, occurs on similar sites in the New Jersey pine barrens; at the latitude of the Outer Banks, *P. rigida* occurs in the mountains and upper Piedmont only. *Quercus ilicifolia* has a similar pattern of distribution. Distributional data were compiled for all native Outer Banks species from ranges listed in Fernald (1950) and Radford, Ahles, and Bell (1964). Of the 462 native species occurring on the Outer Banks, 418 range south to Florida; 172 range from Maine to Florida; and 23 range north to Maine but not south to Florida. Obviously not all native Outer Banks species which range north to Maine occur on lower Cape Cod, and their exclusion from the Cape Cod flora may be, in large part, accidental.

Any attempt to evaluate the floristic relationships of these coastal areas must consider the relative ease with which plants can become established, thrive, and then quickly disappear on physiographically unstable sites. Changes in the distribution of the stemless palmetto, *Sabal minor,* on the Outer Banks, have been elsewhere recounted (Burk, 1966). Other abrupt changes in the status of various species within the Cape Cod or Outer Banks floras have been noted. Camphorweed, *Heterotheca subaxillaris,* was collected by A. E. Radford from the Cape Hatteras area prior to my own work there. A search of Hatteras Island in 1959 and 1960 yielded no camphorweeds, yet in the spring of 1961 they were found well-established in the vicinity of the Hatteras light, an area which had not been overlooked the year before. The naturalist on the staff of the Cape Hatteras National Seashore reported that camphorweeds, with which he had been previously unfamilar, had first appeared near the Hatteras Light that spring. Camphorweeds also became established on Roanoke Island during that period; they were still persisting in the vicinity of the Hatteras Light four years later. On Cape Cod in the "Provincelands" area near Provincetown, the Christmas fern, *Polystichum achrostichoides,* appeared during the summer of 1966. The station for this fern nearest to the Provincelands is more than 50 miles distant.

Table 2 lists the number of native species, genera, families, and orders found on lower Cape Cod and the Outer Banks, the number of these taxa shared by the two areas, and an "index of floristic resemblance". This index (100 C/N_1 in which C stands for the number of taxonomic units common to the two floras and N_1 is the total number of units in the smaller of the two) is useful because its value is little affected if one flora differs from another in occupying a region of more diverse environments (Simpson, 1965) and should be more widely used in phytogeographic work. Its use in zoogeography is discussed in some detail by Simpson (1943, 1947). The total shared native species represent 132 genera, not all shared genera being represented by the same species in the two areas. Concepts of the various taxa follow Fernald (1950) except in the relatively few instances in which a species lies outside the range of his manual; hence similarities or dissimilarities here noted in the flora basically reflect the presence or absence of taxonomic entities rather than differences in the judgement of taxonomists as to the limits of these entities. Radford, Ahles, and Bell (1964) was consulted for the species outside the range of Fernald.

Cape Cod, with its considerably larger number of species than the Outer Banks, has very nearly the same number of genera and fewer families and orders. The *generic coefficient* (total genera/total species × 100) of Cape Cod is 48; the generic coefficient of the Outer Banks is 60. To some extent, this difference reflects the abundance of polyspecific genera on Cape Cod, their scarcity on the Outer Banks and, in turn, the greater ecological diversity of lower Cape Cod compared with the Outer Banks. Only four Outer Banks genera (*Cyperus, Juncus, Panicum,* and *Quercus*) are represented on the Outer Banks by 8 or more species; 11 genera *(Aster, Carex, Cyperus, Dryopteris, Eleocharis, Juncus, Panicum, Polygonum, Rubus, Scirpus,* and *Solidago)* have 8 or more species on Cape Cod.

Table 3 lists the percentages of the total native floras of Cape Cod, the Outer Banks, and the area of Fernald

Table 3. Percentage of total native floras on lower Cape Cod, the Outer Banks, and the area of Fernald (1950) represented by the three largest families on lower Cape Cod and the Outer Banks and the generic coefficient of each family within each flora.

family	% of total native flora			generic coefficient		
	Cape Cod	Outer Banks	Fernald	Cape Cod	Outer Banks	Fernald
Cyperaceae	11.6	8.0	10.2	16.2	32.4	3.8
Compositae	11.3	13.4	12.7	40.9	48.9	14.5
Gramineae	9.6	14.7	8.8	55.4	58.6	19.3

(1950) represented by Cyperaceae, Compositae, and Gramineae, which are, though not always in that order, the three largest families on both lower Cape Cod and the Outer Banks, and the generic coefficient for each family within each flora. The percentages of the total floras comprised by those families are not greatly different in the three areas. The generic coefficients are markedly higher in the coastal regions than throughout the larger range, reflecting again a greater ecological diversity in the larger range, as well as simply greater area. In all instances, however, the generic coefficient of each family is higher on the Outer Banks than on Cape Cod. The Cyperaceae, with the lowest coefficient in both areas, is the largest of the three families on lower Cape Cod and the smallest of the three on the Outer Banks. Hence, it would appear that ecological diversity, total area, and the relative abundance of families or genera with markedly high or low generic coefficient are factors determining the generic coefficient of any flora. Nonetheless, one would still expect to find increased rates of speciation (and hence a lower coefficient) in more recently assembled floras and lower rates of speciation (and hence a higher coefficient) in older, well-established floras.

Table 4 lists the number of non-native species, genera, and families occurring on lower Cape Cod and the Outer Banks, the number of these taxa shared, and the index of floristic resemblance. Lower Cape Cod has a greater percentage of non-native species in its total flora (20.3%) than does the Outer Banks (17.1%) or eastern United States above Virginia (19.9% in Fernald, 1950). On Cape Cod,

Table 4. Non-native species, genera, and families occurring on lower Cape Cod, the Outer Banks, taxa shared by both areas, and an index of resemblance.*

	Species	Genera	Families
lower Cape Cod	149	110	42
Outer Banks	95	55	33
Shared (both native)	32	38	24
index	33.7	69.1	72.7

*see text

several non-native species including *Rosa rugosa, Artemesia stelleriana,* and *Ammophilla arenaria* are common in salt-spray influenced communities. On the Outer Banks the only well-established non-native species are *Gaillardia pulchella* and *Phlox drummondii,* escaped cultigens found chiefly near habitations.

The non-native floras do not differ greatly from the native floras in their degree of resemblance. This similarity results, in all probability, from the fact that plants tend to become established in areas ecologically not unlike those to which they are native. The origins of the non-native species are summarized in Table 5. The data on the area

Table 5. Percentages of species in the non-native floras of lower Cape Cod and the Outer Banks originating in the Old World, tropical America, and other areas.

	Cape Cod	Outer Banks
Old World (mostly Europe, Asia or Eurasia)	92.5%	81.0%
Tropical America	1.3%	14.7%
Other (Australian, western North America, unknown, tropical cosmopolitan)	6.1%	4.3%

of origin for each species were taken from Fernald (1950) or Bailey (1949). A marked tropical American element present in the non-native flora of the Outer Banks is virtually lacking on lower Cape Cod. The generic coefficient of non-native species on Cape Cod (74) is higher than that of the Outer Banks (61).

An attempt was made to determine the successional community in which the shared species occur. Many of the shared species occur with a rather low degree of fidelity in several communities. However, the greatest number of species common to both Cape Cod and the Outer Banks occurs in the tidal marshes, a fact to which even a relatively casual observer could attest. The dominant forest genera *Pinus* and *Quercus* are represented by different species in each area. On Cape Cod, *Pinus rigida*, *Quercus velutina*, and *Q. alba* are found on drier sites than their counterparts *Pinus taeda*, *Quercus falcata*, *Q. nigra*, and *Q. laurifolia* on the Outer Banks where the rainfall is more abundant. *Fagus grandifolia* occurs in both areas, as do *Acer rubrum* and *Nyssa sylvatica*. *Diospyros virginiana* and *Ilex opaca*, common elements in the Outer Banks forests, are at or near their northern limits on Cape Cod.

Quercus virginiana, a dominant member of the shrub community on the Outer Banks, is tolerant to salt-spray but intolerant to shading and hence usually excluded from the mature forest community. On Cape Cod, *Quercus ilicifolia*, a member of a different subgenus from *Q. virginiana*, occupies a similar niche. On the Outer Banks, *Quercus nigra*, *Q. phellos*, and *Q. laurifolia* form an elaborate hybrid complex (Burk, 1961, 1963) and might well, in that part of their range, be considered one widely-varying species. On Cape Cod, *Quercus velutina* is equally variable; studies have shown that, in part, this variability has resulted from hybridization and introgression with *Q. ilicifolia*. On Nantucket Island, populations of *Q. ilicifolia* show almost certain evidence of introgression with *Q. falcata* which is at its northern limit there (Bicknell, 1909). If forests similar to those in North Carolina were present on Cape Cod during the recent thermal maximum, as they were during other interglacial periods (Dorf, 1960), their replacement by more northerly elements has almost certainly not been catastrophic but rather a gradual exclusion, resulting in relict populations which, while diminishing, often hybridize and introgress with their successors.

CAPE COD AND THE OUTER BANKS AS FLORISTIC POINTS OF DEMARKATION

Dunbar (1958), commenting on W. W. Ashe's statement that coastal or maritime forests could be roughly separated into two divisions at Cape Hatteras, concludes, quite correctly, that "Actually the floral changes are not really very abrupt. As one goes north along the coast, the southern species drop out one by one. Similarly, as one goes southward, the northern species decline. It is interesting, however, that so many of the southern plants are so well represented on the Outer Banks, not far from their absolute northern limit." He lists *Ilex vomitoria, Quercus virginiana, Sabal minor, Tillandsia usneioides,* and *Zanthoxylum clava-herculis* as examples of plants showing this distribution pattern.

The following plant species reach their southernmost point of distribution on the Outer Banks: *Hudsonia tomentosa, Ammophila breviligulata,* and *Juncus articulatus.* The first two of these are prominent in the dune-grass community northward from the Banks. A number of species apparently reach their northern limits on the Banks. These include *Sabal minor, Prunus caroliniana, Smilax auriculata, Yucca aloifolia, Yucca gloriosa, Croton punctatus, Helianthemum corymbosum, Gaura angustifolia, Ludwigia maritima, Hydrocotyle bonariensis,* and *Ipomea sagittata.*

All species whose distributional limits are reached on Cape Cod are southern species at their northern limits, with the exception of *Suaeda richii,* which reaches its southernmost limit on Cape Cod. These include *Diospyros virginiana, Cyperus polystachyos, Juncus biflorus,* and *Spartina cynosuroides.* If Nantucket Island is included as a part of the Cape Cod area, *Quercus falcata, Smilax bona-nox, Lycopodium carolinianum,* and *Ascyrum hypericoides* may be added to this list. A number of species reach their northernmost limit in southeastern Massachusetts in the vicinity of the Cape, including *Quercus stellata, Ilex opaca,* and *Juncus dichtomous.*

The large number of species reaching their northernmost point of distribution on either Cape Cod or the Outer Banks results, in large part certainly, from the fact that the climates of these areas, as previously noted, is milder than the adjacent mainland. Cape Cod and the Outer Banks are, in effect, northward islands of more southerly climates. If there was a thermal maximum, elements of the floras on Cape Cod and the Outer Banks must be relicts of that period. Relicts from the thermal maximum along the coast north of Boston where the postglacial rise in sea-level covered the present shoreline would have been, in large part, drowned.

SMITH COLLEGE
NORTHAMPTON, MASSACHUSETTS 01060

LITERATURE CITED

BAILEY, L. H. 1949. Manual of Cultivated Plants. The MacMillan Company, New York.

BICKNELL, E. P. 1909. The ferns and flowering plants of Nantucket-IV. Bull. Torrey Bot. Club **36**: 1-29.

BOYCE, S. G. 1954. The salt-spray community. Ecol. Monog. **24**: 29-67.

BURK, C. J. 1961. A Floristic Study of the Outer Banks of North Carolina. Unpublished PhD thesis, U. of North Carolina, Chapel Hill, N.C.

——— 1962a. The North Carolina Outer Banks: a floristic interpretation. Jour. Elisha Mitchell Sci. Soc. **78**: 21-28.

——— 1962b. An evaluation of three hybrid-containing oak populations on the North Carolina Outer Banks. Jour. Elisha Mitchell Sci. Soc. **78**: 18-21.

——— 1963. The hybrid nature of *Quercus laurifolia*. Jour. Elisha Mitchell Sci. Soc. **79**: 159-163.

——— 1966. Dynamics of plant distribution I — *Sabal minor*. Advancing Frontiers of Plant Sciences **14**: 1-4.

CHAMBERLAIN, B. B. 1964. These Fragile Outposts. Natural History Press, Garden City, N.J.

DAVIS, M. B. 1965. Phytogeography and palynology of Northeastern United States in Wright, H. E. and D. G. Frey, eds. The Quarternary of the United States, Princeton U. Press, Princeton, N.J. 377-401.

DEEVEY, E. S., JR. and FLINT, R. F. 1957. Postglacial hypsithermal interval. Science **125**: 182-184.

DORF, ERLING. 1960. Climatic changes of the past and present. American Scientist **48**: 341-364.

DUNBAR, G. S. 1958. Historical Geography of the North Carolina Outer Banks. Louisiana State U. Press, Baton Rouge, La.

ENGELS, W. 1952. Vertebrate fauna of North Carolina coastal islands. II Shackleford Bank. Am. Midl. Nat. **47**: 702-742.

FERNALD, M. L. 1950. Gray's Manual of Botany, 8th Edition. American Book Company, New York, N.Y.

HINDS, H. R. 1966. A Floristic Study of Outer Cape Cod, Massachusetts. Unpublished Masters thesis, Smith College, Northampton, Massachusetts.

RADFORD, A. E., H. E. AHLES and C. R. BELL. 1964. Guide to the Vascular Flora of the Carolinas. The Book Exchange, U. of North Carolina, Chapel Hill, N.C.

RAUP, H. M. 1937. Recent changes in climate and vegetation in southern New England and adjacent New York. Jour. Arnold Arboretum **18**: 79-117.

RICHARDS, H. G. 1950. Geology of the Coastal Plain of North Carolina. American Philosophical Soc., Philadelphia, Pa.

SCHAFER, J. P. and J. H. HARTSHORN. 1965. The Quaternary in New England in Wright, H. E. and D. G. Frey, eds. The Quaternary of The United States. Princeton U. Press, Princeton, N.J. 113-128.

SIMPSON, G. G. 1943. Mammals and the nature of Continents. Amer. Jour. Sci. **241**: 1-31.

——————— 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. Amer. **58**: 613-688.

——————— 1965. The Geography of Evolution. Chilton Co., Philadelphia, Pa.

USDA YEARBOOK. 1941. Climate and Man. Government Printing Office, Washington, D.C.

WHITEHEAD, D. R. Palynology and Pleistocene phytogeography of unglaciated North America in Wright, H. E. and D. G. Frey, eds. The Quaternary of the United States. Princeton U. Press, Princeton, N.J. 417-432.